ORIGINAL ARTICLE

Predicting the sign of trophic effects: individual-based simulation versus loop analysis

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Abstract
Food web research needs to be predictive in order to support decisions system-based conservation. In order to increase predictability and applicability, complexity needs to be managed in such a way that we are able to provide simple and clear results. One question emerging frequently is whether certain perturbations (environmental effects or human impact) have positive or negative effects on natural ecosystems or their particular components. Yet, most of food web studies do not consider the sign of effects. Here, we study 6 versions of the Kelian River (Borneo) food web, representing six study sites along the river. For each network, we study the signs of the effects of a perturbed trophic group i on each other j groups. We compare the outcome of the relatively complicated dynamical simulation model and the relatively simple loop analysis model. We compare these results for the 6 sites and also the 14 trophic groups. Finally, we see if sign-agreement and sign-determinacy depend on certain structural features (node centrality, interaction strength). We found major differences between different modelling scenarios, with herbivore-detritivore fish behaving in the most consistent, while algae and particulate organic matter behaving in the least consistent way. We also found higher agreement between the signs of predictions for trophic groups at higher trophic levels in sites 1–3 and at lower trophic levels in site 4–6. This means that the behaviour of predators in the more natural sections of the river and that of producers at the more human-impacted sections are more consistently predicted. This suggests to be more careful with the less consistently predictable trophic groups in conservation management.

Abbreviations

ALGA	Green and blue-green algae
CARN	Carnivorous fish
COLF	Invertebrate collector-filterers
COLG	Invertebrate collector-gatherers
DIAT	Diatoms
FILA	Filamentous bacteria
GRAZ	Invertebrate grazers
HEDE	Herbivore-detritivore fish
HERB	Herbivorous fish
HUMW	Human waste
LEAF	Leaf litter
OMNI	Omnivorous fish
POM	Settled and suspended coarse and fine Particulate Organic Matter
PRED	Invertebrate predators
SHRE	Invertebrate shredders
TERR	Terrestrial insects

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Introduction

In complex ecological systems, the multiplicity of direct and indirect interactions makes it difficult to provide simple and clear predictions on the effect of single-node perturbations. The effects on other organisms and, generally, community response are the outcome of a number of interconnected pathways. Predicting whether the influence of organism i on organism j will be positive or negative is not easy, even without considering non-trophic effects and complicated functional responses. Also, the experimental results on positive inter-specific interactions are still quite sporadic (Bertness & Shumway, 1993; Bruno et al., 2003; Kareiva & Bertness, 1997) compared to the mass of literature on competition and predation. Considering effect sign is critically important if food web models are to be extended to ecological interaction networks: this is the way how to complete antagonistic

predator–prey interactions with positive feedback loops (Dong et al., 2020; Ulanowicz, 1995) and mutualisms (Leemans et al., 2020).

Network analysis offers various methods for predicting effect sign. Loop analysis (Levins, 1974; Puccia & Levins, 1985a), mixed trophic impact (Bondavalli & Ulanowicz, 1999; Ulanowicz & Puccia, 1990), signed topological importance (Liu et al., 2010, 2020) and dynamical simulations (Jordán et al., 2012) can be used but their relationship is not straightforward (i.e. whether they provide similar or complementary information). Yet, loop analysis has been used extensively together with topological network analysis (e.g. Ortiz et al., 2013, 2015, 2017).

Generally speaking, topological models provide fast and easy but not very realistic results: they consider only the existence of network links (in a binary way) or also their directionality and the weights on them (in more detailed network models) but do not reflect the dynamical behaviour (parameters, kinetics) of the network. Sophisticated food web simulations may provide more accurate results but typically need a lot of data (dynamical parameters) and the interpretation of results raises questions about indeterminacy (Yodzis, 1988), uncertainty (Geary et al., 2020), additivity (Móréh et al., 2021) or whether the system is close to equilibrium (Baker et al., 2017). Qualitative models, like loop analysis, are somewhere in between, trying to combine simplicity (without explicit dynamics) and reality (interaction sign considered).

In this paper, we study food webs at the level of individual nodes (trophic groups), at the level of the interactions among the trophic groups and at the level of the whole networks. We compare (1) the results of loop analysis and dynamical simulations predicting the sign of effects following single-node perturbations. Beyond comparing the signs of the predictions in these two methods, we also compare (2) the 6 food web models as well as (3) the 14 trophic groups. Finally, (4) we investigate if there is a correlation between the network centrality of a trophic group and the sign-agreement between the two models predicting its effects on other groups.

Data and methods

Data

We used 6 versions of the Kelian River (Borneo) food web for our analysis (data from Yule, 1995; Yule et al., 2010). This makes it possible to assess spatial variability within the ecosystem.

The food web is described for 6 different locations along the river (Jordán et al., 2012, 2017), based on extensive earlier field work (Yule, 1995; Yule et al., 2010). The 6 sites

represent a gradient from a pristine rainforest to a human settlement. The pristine food web (site 1) contains 14 trophic groups and 2 additional groups appear only downstream, so the total number of trophic groups is 16 (see Table 1). Most of the groups represent living organisms (e.g. PRED: invertebrate predators) but there are some non-living groups as well (e.g. POM: settled and suspended coarse and fine Particulate Organic Matter). The definition of the groups and the description of interactions among them are based on long-term, extensive field work (Yule, 1995; Yule et al., 2010).

Food web structure: topological importance

We quantified the network centrality of trophic groups by the topological importance index (TI). This method is based on an earlier measure (Müller et al., 1999) for 2-step-long apparent competition in host-parasitoid communities, later generalized for n-step-long indirect effects in Jordán et al. (2003). Consider that i and j are connected (prey and predator), and the direct effect of i on j (a_{ij}) is as follows:

$$a_{ij} = 1/D_j \qquad (1)$$

where D_j is the degree of node j (the number of direct neighbours). So, if i is the only neighbour of j, its effect will equal 1 (the maximum), but if j has more neighbours, the effect of i will be smaller. We can put this direct effect between all pairs of nodes in a matrix A, and generalize it to an n-steps effect just by calculating A^n. As different paths of different lengths between two nodes may exist, we can calculate the

Table 1 The abbreviation for the 16 trophic groups composing the 6 food webs

ALGA	Green and blue-green algae
CARN	Carnivorous fish
COLF	Invertebrate collector-filterers
COLG	Invertebrate collector-gatherers
DIAT	Diatoms
FILA	Filamentous bacteria
GRAZ	Invertebrate grazers
HEDE	Herbivore-detritivore fish
HERB	Herbivorous fish
HUMW	Human waste
LEAF	Leaf litter
OMNI	Omnivorous fish
POM	Settled and suspended coarse and fine Particulate Organic Matter
PRED	Invertebrate predators
SHRE	Invertebrate shredders
TERR	Terrestrial insects

effects of node i on j, up to a defined number of steps, and then average them over the maximum number of steps considered (i.e. n):

$$\mathrm{AE}_{n,ij} = \frac{1}{n}\left(A_{ij} + A_{ij}^2 + A_{ij}^3 + \ldots A_{ij}^n\right)$$

with this average effect of all pairs in the network, we can construct an interaction matrix IM^n, where the ijth element is the $\mathrm{AE}_{n,ij}$. Then, the sum of the values in ith row is the topological importance of i, as it is the sum of effects up to n-steps on the other nodes of the network.

Based on indirect chain effects, we can assume that central species of interaction networks are of higher importance for the rest of the community (Jordán et al., 2006). This is one approach to the quantification of key (possibly keystone) species in food webs. The centrality of species (trophic groups) in food webs seems to be a systemic property with important ecological correlates (e.g. body size, mobility, see: Olmo Gilabert et al., 2019). There are a number of topological indices quantifying centrality in networks and their relationship is increasingly understood (Scotti et al., 2007). Since we must deal with indirect effects in order to assess the combinations of positive and negative impacts, we use the TI index, explicitly considering the length of direct and indirect pathways in food webs (Jordán et al., 2003). We note that TI is an useful centrality measure out of the many, according to a recent study where machine learning identified the most predictive combinations of centrality indices (Gouveia et al., 2021). In this paper, we used TI^3, i.e. we considered indirect effects up to 3 steps. We performed these calculations in order to see whether there is structural basis of (constraints on) the sign-agreement (for nodes and networks) and sign-determinacy (for interactions and networks).

Loop analysis

Loop analysis is a qualitative method that uses signed digraphs to illustrate networks of interacting variables (Levins, 1974; Puccia & Levins, 1985a). This technique gives the opportunity to represent the structure of linkages of the variables and the patterns of their variations (Bodini & Clerici, 2016; Dambacher & Ramos-Jiliberto, 2007). Also, these models allow to examine the effect of non-biological variables on our system (such as gold mining, fishing etc.). This qualitative modelling approach provides a method that is useful where species and their natural history are well-known, but not quantified (Dambacher et al., 2003).

Signed digraphs are based on the generally accepted interactions between nodes (trophic groups). These interactions come from the previous trophic models in Jordán et al. (2012). The figures show two types of connections: arrows ($\rightarrow$) for positive and circle-head links ($-$o) for negative
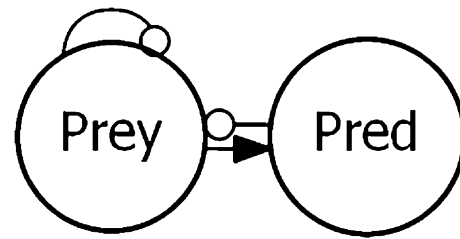

Fig. 1 Signed digraph of a simple prey–predator system. The prey affects positively the predator ("Pred"), indicated by a black arrow. Empty circles indicate negative effects: from the predator to the prey and the self-effect of the prey

effects. These links are originated from the coefficients of the community matrix (Levins, 1974). The diagonal terms of the community matrices are self-effects on system variables, represented in signed digraphs as links connecting variables with themselves. These links are self-dampening (circle-headed) with self-limiting growth rate. For a simple prey–predator system, see Fig. 1.

Using the qualitative modelling framework of loop analysis, one can analyse pathways and feedbacks in the system, making predictions about the response of variables to perturbations. These can be the addition (increased biomass) or deletion (decreased biomass) of other nodes. Based on feedbacks and pathways, one can qualitatively specify the direction of changes.

We followed the method described in Bodini and Clerici (2016) to get the predictions for our networks. The loop formula is used for calculating the equilibrium value of the variables following a perturbation, so it can be deduced how does the abundance of a certain variable change (Bodini, 2000):

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k}\left\lfloor \frac{\delta f_i}{\delta c}\right\rfloor \times \left[p_{ji}^{(k)}\right] \times \left[F_{n-k}^{(\mathrm{comp})}\right]}{F_n}$$

On the left side, x_j is the variable with the equilibrium value being calculated and c is the changing parameter (e.g. mortality, fecundity, abundance). On the right side, f is the growth rate, $\partial f_i/\partial c$ designates whether the growth rate of the ith variable is increasing or decreasing (positive or negative input, respectively), $p_{ji}^{(k)}$ is the pathway connecting the variable to the changed biomass variable (where the perturbation enters the system), $F_{n-k}^{(\mathrm{comp})}$ is the complementary feedback, which buffers or reverses the effects of the pathway and F_n designates the overall feedback of the system, which is a measure of the inertia of the whole system to change (Bodini, 2000; Bodini & Clerici, 2016). See also (Puccia & Levins, 1985a) for the discussion of the correspondence between matrix algebra and loop analysis.

The net effect (the sum of the direct and indirect effects) on variable i resulting from a perturbation on variable j is given by the $j-ith$ element of the inverse community matrix $[A]^{-1}$ (see Levins, 1974; Puccia & Levins, 1985b; Raymond et al., 2011). The sign of the coefficients of $[A]^{-1}$ gives the direction of the expected changes for the variables (Bodini & Clerici, 2016). To make predictions, we used a routine that randomly assigns numerical values from an uniform distribution to the coefficients of the community matrix (these coefficients belongs to the links of the signed digraph). This was performed $100*N^2$ times, where N is the number of variables in the system. Matrices satisfying the asymptotic Lyapunov criteria were accepted and inverted. The routine of Bodini and Clerici (2016) calculated predictions for the probabilities based on the percentage of positive and negative signs and zeroes in the inverted matrices. They defined

a set of rules to make a final table of predictions only from signs (Table 2, Bodini & Clerici, 2016).

Community matrices show the links between the trophic groups. The elements in the rows affect the elements in the columns and the values could be -1, 0 or 1. These represent prey–predator (resource-consumer) effects. We decided to work with self-dampening variables only for living groups (see Table 3 for the community matrix of site 1).

We were interested in the effect of decreasing the biomass of each trophic group (i.e. the value of each variable), one by one. For this, we needed to simply reverse our predictions (change signs from $+$ to $-$) (Dambacher et al., 2002). By predicting these changes, qualitative models can also predict the correlation patterns between the examined groups/variables (Bodini, 2000; Bodini & Clerici, 2016; Puccia & Levins, 1985a).

Levins' loop algorithm was extended in Dambacher et al. (2002) to complex ecological systems. The adjoint of the negative of this community matrix shows the net number of complementary feedback cycles. A complementary feedback appears if k variables in the path are ideally excluded from the graph: what remains is called the complementary subsystem. The complementary feedback is the feedback that groups all the variables in the complementary subsystem (Bodini & Clerici, 2016) that contribute to the responses of other variables in the whole system. Therefore, the adjoint of the $-°A$ is equivalent to Levins' loop analysis algorithm and its relation with the inverse matrix (A^{-1}) is as follows:

Table 2 The frequency of positive ("+") effects in the inverted matrices defines the sign of predictions

% of "+"	sign
0–24	$-$
25–39	$?-$
40–59	$0*$
60–74	$?+$
75–100	$+$
% of "0" = 100	0

Half of the effects correspond to clear predictions on the sign of effects (lower 25% for negative and top 25% for positive prediction). Less than a third of the effects correspond to weak predictions (15–15% for both weak negative and weak positive predictions). The fifth of the effects (the middle 20%) correspond to net zero prediction ("0*"). Finally, "0" means no change in the abundance of the variable (Bodini & Clerici, 2016)

$$-A^{-1} = \frac{\text{adjoint}(-A)}{\text{determinant}(-A)} \qquad (2)$$

Table 3 Community matrix for site 1

	ALGA	CARN	COLF	COLG	DIAT	GRAZ	HEDE	HERB	LEAF	OMNI	POM	PRED	SHRE	TERR
ALGA	-1	0	0	0	0	1	1	1	0	1	0	0	0	0
CARN	0	-1	-1	-1	0	-1	-1	-1	0	-1	0	-1	-1	-1
COLF	0	1	-1	0	0	0	0	0	0	1	-1	1	0	0
COLG	0	1	0	-1	0	0	0	0	0	1	-1	1	0	0
DIAT	0	0	0	0	-1	1	1	1	0	1	0	0	0	0
GRAZ	-1	1	0	0	-1	-1	0	0	0	1	-1	1	0	0
HEDE	-1	1	0	0	-1	0	-1	0	-1	0	-1	0	0	0
HERB	-1	1	0	0	-1	0	0	-1	0	0	-1	0	0	0
LEAF	0	0	0	0	0	0	1	0	0	0	0	0	1	0
OMNI	-1	1	-1	-1	-1	-1	0	0	0	-1	-1	-1	-1	-1
POM	0	0	1	1	0	1	1	1	0	1	0	0	0	0
PRED	0	1	-1	-1	0	-1	0	0	0	1	0	-1	-1	0
SHRE	0	1	0	0	0	0	0	0	-1	1	0	1	-1	0
TERR	0	1	0	0	0	0	0	0	0	1	0	0	0	-1

Direct trophic interactions are represented in such a way that the elements in the rows affect the elements in the columns and the values could be -1, 0 or 1, depending on field data. We decided to work with self-dampening variables only for living groups

where the adjoint and inverse matrices are calculated with the negative of the community matrix, thus the positive input is read down the columns and the responses along the rows (Dambacher et al., 2002). The adjoint quantifies the results of the prediction tables, so their numerical values make correlation tests possible in further analyses.

An "absolute feedback" matrix was defined in Dambacher et al. (2002) to calculate the absolute number of complementary feedback cycles in a response whether positive or negative:

$$T_{ij} = \text{permanent}\left(\text{minor} \cdot A_{ij}\right) \tag{3}$$

where $\dot{A}$ denotes the adjacency matrix (absolute values of $°A$). Complementary feedback cycles are needed to express the equilibrium response of community members by inverting the direct effects of the community matrix (Dambacher et al., 2003).

The "weighted predictions" matrix can be calculated from Eqs. (1)–(2):

$$W = \frac{\overrightarrow{|adj°A|}}{T}$$

where "→" is a vectorized matrix operator, what denotes element-by-element division ($W_{ij} = 1$, when $T_{ij} = 0$). The elements of W show the probability of sign-determinacy of response predictions in the adjoint matrix. If all of them are of the same sign in one cell, then $W_{ij} = 1$. If there is an equal number of negative and positive feedback cycles, then $W_{ij} = 0$ (Dambacher et al., 2002). The $W_{ij} = 0.5$ value is a threshold for sign-determinacy in models of any size (Dambacher et al., 2003).

We used the adjoint values to investigate if sign-determinacy depends on the strength of interactions (based on both structure and simulations).

Dynamical simulations

For the dynamical simulation data on the food webs, we used earlier results of an individual-based model (Jordán et al., 2012, 2017). This simulation model was built in the process algebra-based language, BlenX (Jordán et al., 2011): abundance was calculated for the trophic groups and interaction strength was converted to probability, according to the kinetics of the stochastic simulation framework used routinely in systems biology (Dematté et al., 2008; Gillespie, 1977; Priami, 2009; Priami & Quaglia, 2004).

The stochastic IBM simulation model was parameterized with field data (e.g. abundance data, Yule, 1995; Yule et al., 2010) and was balanced by a genetic algorithm. Following the reference runs, sensitivity analysis was performed. The abundance of each trophic group was perturbed, and the response of each other trophic group was measured. Since this was a stochastic model, both the mean and the variability were evaluated (for the details, see Jordán et al., 2012, 2017).

In this paper, we used only the sign of the responses (not their strength). For comparability, minimal changes must be made in the results of the dynamical simulations: since these categories do not exist in simulations, ?+, ?− and 0* predictions were considered as +, − and 0, respectively. Further, as the effects in dynamical simulations never result exactly in 0, we needed to define zero effects during the simulations. For this, we needed a threshold level below the effect can be considered zero. Instead of using an arbitrary threshold, we decided to set the threshold in such a way that the number of zeroes equals the number of zero responses in loop analysis. Values in this "corridor" of the smallest positive and negative simulation outcomes were considered 0.

Software

We used MASS 7.3–51.5 and nlme 3.1–148 *R* packages for the analyses. For simulating sign predictions, we used the *R* code in Bodini and Clerici (2016). The LoopAnalyst 1.2–6 package was used for the calculations of the adjoint of the -$°A$ and the "weighted predictions" matrices (and it required the nlme package, too). Figures 2 and 3 are created with GVEdit Graph File Editor For Graphviz version: 1.02 and Graphviz version:2.38.

Statistical methods

Sign-agreement was examined on several levels. We compared the predictions of loop analysis to the calculations made by the structural importance index TI[3] and to the results of dynamical simulations for the whole networks, for individual nodes (i.e. the rows of the matrices) and for individual interactions.

As described above, we categorized the mean outcome of dynamical simulation results into 3 categories (+, 0, −). This way, the table of predictions from loop analysis and the matrix of simulation effects became comparable (both containing only +, − and 0). A binary sign-agreement matrix contained 1 (yes) for similar and 0 (no) for different signs in the two matrices. The percentage of 1 values served for quantifying sign-agreement (1 s in the main diagonal, corresponding to self-effects, were not considered).

Chi-square tests were applied for the effect signs for each node, determining if there is significant difference in either loop analysis or dynamical simulations.

In order to see if there is some structural basis for sign-determinacy and sign-agreement, we tested the correlation

Fig. 2 Food web of the Kelian River ecosystem in sites 1–6 (**a**–**f**). The arrow shows the consumer, and the circle shows the resource for each trophic flow (who eats whom). Trophic groups are arranged according to trophic height
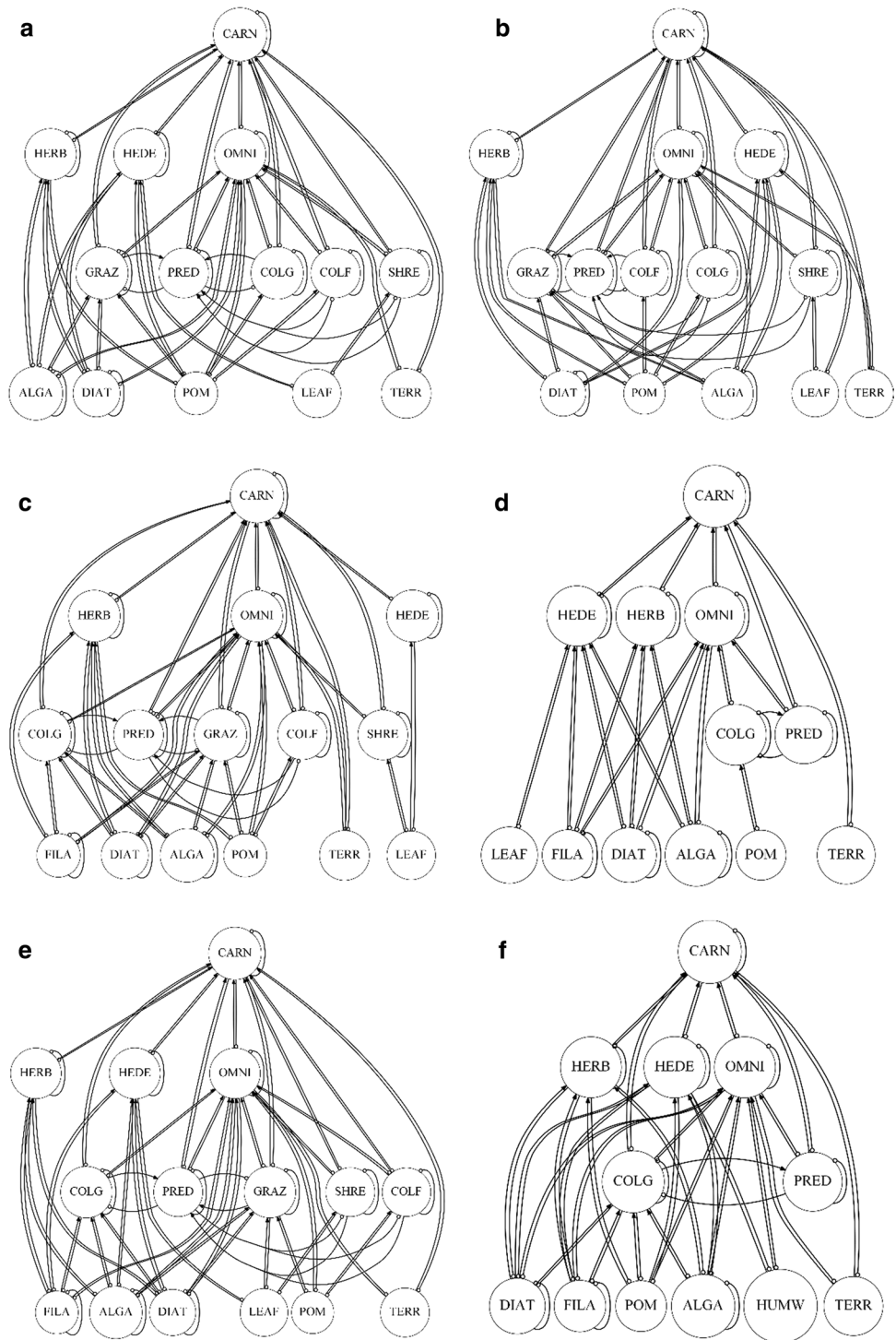

between (1) the adjoint matrix and the dynamic simulation results at the level of the whole network, (2) the adjoint matrix and interaction strength calculated by TI_{ij} at the level of interactions, (3) the dynamic simulation results and interaction strength calculated by TI_{ij} at the level of interactions and (4) sign prediction of loop analysis and node centrality measured by TI_i at the level of network nodes.

Results

Figure 2 shows the food web for each of the 6 sites. The number of trophic groups varies between 12 and 15, starting from 14 in the pristine forest (site 1).

Our values in the "weighted predictions" matrix were mostly under $W_{ij} = 0.5$. According to this, most of the

Fig. 3 Food web of the Kelian River ecosystem in sites 1–6 (**a**–**f**). Arrows show the predictions of loop analysis: the sign of the effect of decreasing the abundance of a node on another (red is positive, blue is negative). The colour of nodes shows sign-agreement (%) between the predictions of loop analysis and the results of dynamical simulations (increasing from light yellow to dark green). Whether perturbing the light yellow nodes has positive or negative effect on others largely depends on the model chosen (see Table 4). On the contrary, the perturbation of dark green nodes is similarly predicted by both approaches (see Table 4). Coloured by ColorBrewer (Neuwirth & Brewer, 2014)
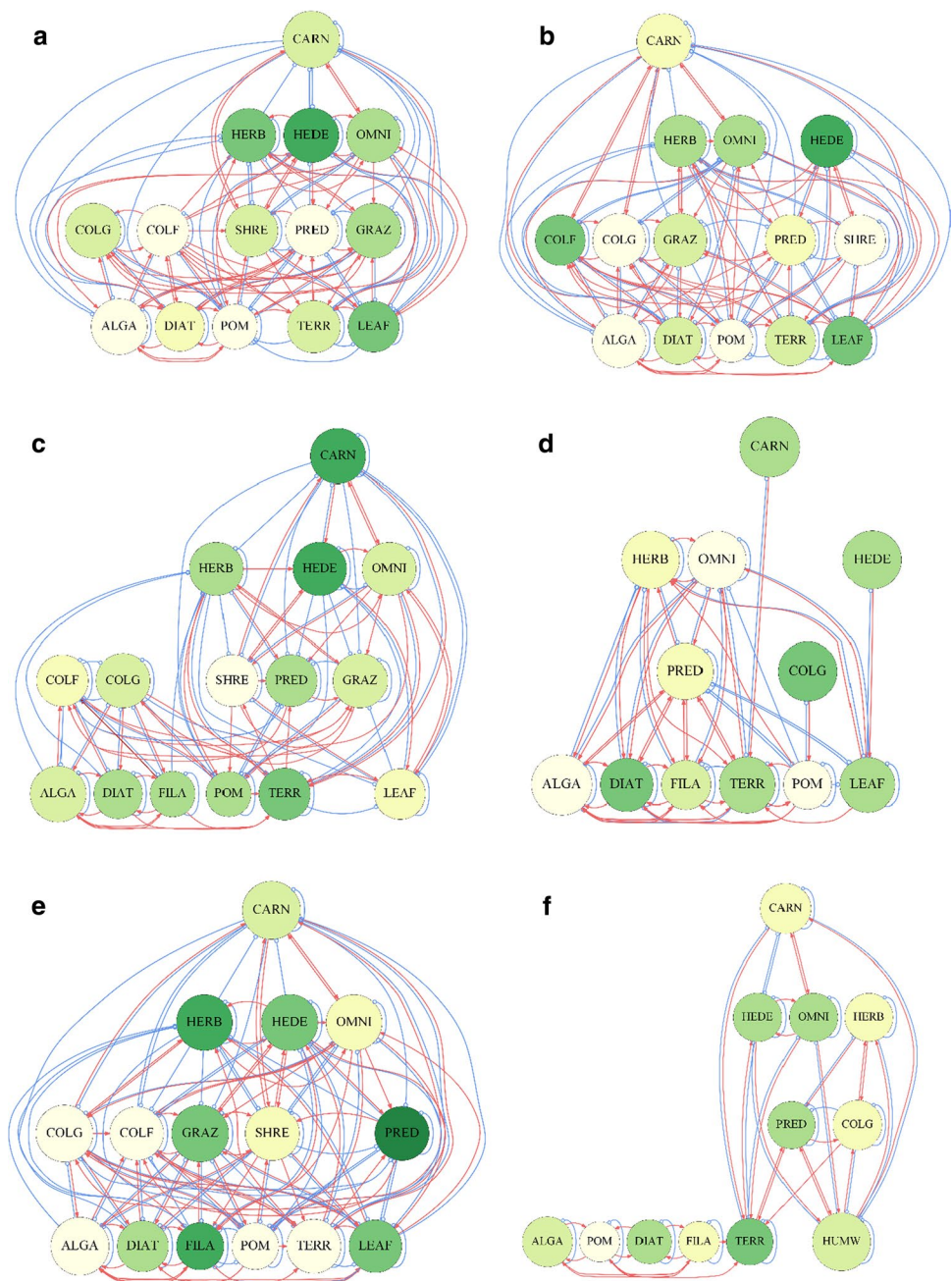
prediction signs were indeterminate. The predicted signs of effects (both clear and weaker predictions) for each trophic group are shown in Fig. 3, for each of the 6 sites (Fig. 3a–f). In site 1 (Fig. 3a), mutually negative (CARN-HEDE), mutually positive (CARN-OMNI), antagonistic (LEAF-GRAZ) unidirectional positive (TERR-PRED) and uni-directional negative (HERB-CARN) interactions can be seen. Between some pairs of trophic groups, there is no interaction predicted (e.g. CARN and COLG). Higher sign-agreement is seen for organisms at higher trophic levels. This pattern seems to be the same also for site 2 (Fig. 3b) but not for the other sites. Site 4 (Fig. 3d) is simpler than the previous sites, with some groups

having only a single interaction partner (e.g. CARN, HEDE, COLG). The differences among the sites are quite characteristic in loop analysis, while the simulation models vary less. Site 6 (Fig. 3f) is strongly dominated by factors essentially external to the stream ecosystem (TERR and HUMW).

Sign-agreement predicted by loop analysis and by the dynamic simulations are shown in Table 4, at the level of the whole networks and for individual nodes (this latter is represented by the colours in Fig. 3: sign-agreement increases from light yellow to dark green). The mean correspondence of signs at the network level is under 50%. Maximum sign-agreement ranged between 50 and

64.29%, and the minimum was between 7.14 and 27.27% (see Table 4). On average, site 6 in the Kelian River is the ecosystem where loop analysis best predicts the signs of dynamical simulation results. From site 2 to site 6, there is a monotonous increase in mean (and the minimal) sign-agreement (the maximum values show no trend and also site 1 is out of this pattern). This suggests that the two methods provide different information on the ecosystem. Some trophic groups generally give consistent behaviour (e.g. HEDE), while others (ALGA, POM) behave differently in different modelling environments. Whether POM will have positive or negative impact on others is differently predicted in 5 out of 6 sites.

Sign-agreement was measured also at the level of the interactions between trophic groups. The mean of sign-agreement is also under 50% but the maximums are between 50 and 72% (Table 5). The high sign-agreement for HEDE is seen also in the interactions in this group, being involved in 4 out of 7 of the highest-agreement interactions. It is also noted that the same group (HEDE) can be involved in minimum (HEDE-POM) and maximum (HEDE-TERR) agreement interactions (see site 2). It is noted that COLG in site 5 has several minimal-agreement interactions (e.g. COLG-POM), after being the most predictable group in site 4 (with the most predictable interaction, COLG-CARN).

The Chi-square tests showed that the predictions of loop analysis for different trophic groups were significantly different only for site 4 of Kelian River (Fig. 4a, see Supplementary 1 for all of the other simulations), while the Chi-square tests for the results of dynamic simulations did not show significant differences (Fig. 4b). Based on loop analysis (Fig. 4a), CARN, COLG and HEDE have predominantly zero and occasionally positive effects on others. On the contrary, TERR (and to some extent POM) have the highest proportion of negative effects. Dynamical simulations (Fig. 4b) show a different outcome with DIAT being the only one without negative effects and HEDE (and ALGA) with the largest negative impacts. According to Supplementary 1, there are significant differences among the distribution of impact signs of various organisms in almost no cases. In

some cases, this homogeneity is quite strong (e.g. site 3, loop analysis with 3 categories), while there are models with non-significant but visible differences (e.g. GRAZ and HEDE in the simulation model of site 2). In the model of site 4, loop analysis with 5 sign categories also provided significant differences among the organisms: the pattern is qualitatively similar to the result of the model with 3 sign categories (see Fig. 4). Only the structural interaction strength (TI_{ij}) and the adjoint values (LA_{adj}) showed significant difference among the various trophic groups in site 4 of the model (see Supplementary 1).

Spearman correlation ($|\rho|$ values) between pairs of simulated interaction strength (a_{ij}), interaction strength based on food web topology (TI_{ij}), node centrality (TI_i), sign-agreement based on loop analysis predictions (LA_{pred}) and the adjoint value based on loop analysis (LA_{adj}) revealed only a single significant correlation (Supplementary 2). In site 4, simulated interaction strength (a_{ij}) correlated with the adjoint (LA_{adj}).

Conclusion

Predictive food web research would be a quantitative and holistic toolkit for systems-based conservation efforts. Good predictions on strong and weak as well as positive and negative effects are important for management and policy. While dynamical simulation exercises require a large number of parameters and complicated models, the semi-quantitative methodology of loop analysis offers simpler (only effect sign) and faster (no temporal simulations) results, generally easier to understand and interpret (under the conditions of close-to-equilibrium situations). Topological analyses are the simplest and least realistic ones. The major question was to what extent and when simpler methods can replace the more complicated ones. We show that for some organisms in some locations (higher trophic levels in more pristine river segments and lower trophic levels in the more human-impacted river segments), the predictions of the different models are in greater agreement. For these cases, one can trust more the model results. In the opposite cases (lower

Table 4 Sign-agreement (between predictions of loop analysis and results of dynamical simulations) for nodes and networks

	Network Min	Network Mean	Network Max	Node Min	Node Max
Site 1	23.08	38.46	61.54	ALGA, COLF, POM, PRED	HEDE
Site 2	7.69	28.57	61.54	ALGA, COLG, POM, SHRE	HEDE
Site 3	14.29	32.86	50	SHRE	HEDE, CARN
Site 4	18.18	36.36	54.55	ALGA, POM, OMNI	COLG, DIAT
Site 5	21.43	38.1	64.29	ALGA, COLG, COLF, POM, TERR	PRED
Site 6	27.27	45.45	63.64	POM	TERR

Mean, minimum and maximum values characterize whole matrices. The trophic groups with minimum (least predictable) and maximum (most predictable) values are shown

Table 5 Sign-agreement (between predictions of loop analysis and results of dynamical simulations) for interactions

	Network Min	Network Mean	Network Max	Interaction Min	Interaction Max
Site 1	19.23	35.71	65.38	ALGA-HERB, ALGA-SHRE, COLF-PRED, POM-CARN, POM-GRAZ	HEDE-COLF
Site 2	3.85	26.53	50	POM-HEDE	HEDE-ALGA, HEDE-TERR
Site 3	7.14	30.67	57.14	COLF-FILA	HEDE-SHRE
Site 4	13.64	33.33	68.18	ALGA-HEDE, OMNI-HEDE, OMNI-TERR, POM-HEDE, POM-TERR	COLG-CARN
Site 5	17.86	35.56	57.14	ALGA-COLG, CARN-COLG, COLF-COLG, POM-COLG, TERR-COLG	PRED-LEAF
Site 6	18.18	41.67	68.18	FILA-OMNI, POM-HERB	TERR-CARN

Mean, minimum and maximum values characterize whole matrices. The inter-specific interactions (direct and indirect effects) with minimum (least predictable) and maximum (most predictable) values are shown
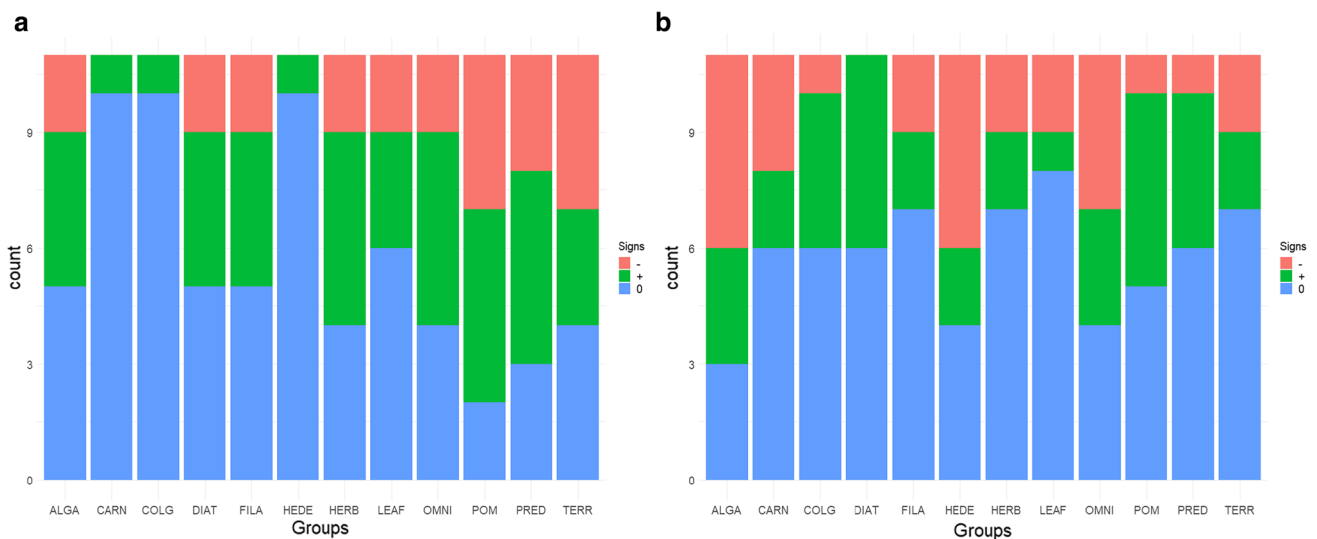
Fig. 4 The number of positive (green), negative (red) and zero (blue) effects. Each 14 functional group are listed along the x axis, and the 13 other are counted along the y axis. This figure represents site 4 of the Kelian River ecosystem model, based on loop analysis (**a**) and dynamical simulations (**b**). In order to make them comparable, the predictions of loop analysis were transformed: we used only 3 categories, + ? was replaced by +, − ? was replaced by − and 0* was replaced by 0. The sign composition of organisms differs significantly in **a** ($\chi^2_{22} = 34{,}67$; $p = 0.04193$) but not in **b** ($\chi^2_{22} = 22{,}989$; $p = 0.4024$). The same plots for other ecosystem models as well as the plots for loop analysis with 6 prediction categories are shown in Supplementary 1

trophic levels in the more pristine river segments and higher trophic levels in the more human-impacted river segments), the predictions are more different, so model results must be more carefully accepted. In these latter cases, more research, better data or a different modelling framework may be needed in order to better support conservation management.

Comparing the sites, we see that the relatively consistent predictability of herbivore-detritivore fish (HEDE) is seen in the sites of otherwise contrasting signs (site 2, site 3). In the middle of the food web, their dynamics may not be extremely affected, or unexpected dynamical effects may be balanced by multiple interactions. The most

consistent interaction happens between terrestrial insects (TERR) and carnivorous fish (CARN) in the most consistent model of site 6. Here, the strong bottom-up dominance in regulation (human waste detritus) simplifies community dynamics but the external input of terrestrial insects remains consumed by carnivorous fish independently of this bottom-up dominance. This is the case when loop analysis and the dynamical simulation model mostly agree on sign prediction.

Based on Table 4, the general pattern emerges that higher sign-agreement is characteristic for trophic groups

at higher trophic levels in sites 1–3, while trophic groups at lower trophic levels in sites 4–6.

Supposing that both models are relevant and correct, the question emerges why and to what extent should they be similar to each other. Similarity means that one reinforces the other, while differences may suggest that they are complementary, providing different kind of information. In the future, mixed trophic impact analysis, signed topological importance and further kinds of dynamical simulations must also be compared to the models studied here. If the predictions of different models agree, one can trust better them, while if results vary, more research or better data are needed. Furthermore, models explicitly addressing uncertainty (Rendall et al., 2021) and predictability (Adams et al., 2020) are becoming increasingly important for supporting conservation management.

It is a question if experimental studies (e.g. mesocosm experiments) could help to better understand the predictability of effect signs and their differences in different modelling environments. Performing experiments only for a few species (e.g. perturbing COLG) might help a lot in calibrating the amount of expected changes and scale the models.

In future research, we need to better understand how trophic complexity is related to predictability, in terms of either interaction strengths or interaction signs. Earlier research, based on time series data, found quite convincing results on the dimensionality of niche space (Stenseth et al., 1997). Also, our research can be extended, for example, towards (1) considering the asymmetry of interactions and (2) considering loop sign (Harary, 1959; Wey et al., 2019). The former could be important in order to better understand cause-effect relationships, as strong asymmetry may imply causality. The latter could help to better assess network-level stability.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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